

American Museum Novitates

PUBLISHED BY THE AMERICAN MUSEUM OF NATURAL HISTORY
CENTRAL PARK WEST AT 79TH STREET, NEW YORK, N. Y. 10024

NUMBER 2303

OCTOBER 20, 1967

New Poeciliid Fishes from Guatemala, with Comments on the Origins of Some South and Central American Forms

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The origins and relationships of the South American poeciliids of the tribe Cnesterodontini are not understood. The tribe was believed by Rosen and Bailey (1963) to be autochthonous in South America, and also to be rather old, as judged by the well-differentiated genera it contains. The recent discovery in central Guatemala of two undescribed poeciliid species, which strongly resemble cnesterodontins superficially but which cannot be assigned to any previously or currently recognized genus in the family, gave promise of contributing new insight into the problem of cnesterodontin affinities. These two new Guatemalan species are described below, and their significance for the tribal classification of the Poeciliidae is discussed.

All the diagnoses, definitions, anatomical terms, and methods of procedure employed here are consistent with those used in our recent revision of the genera of the Poeciliidae (Rosen and Bailey, *ibid.*), and that work should be consulted for details on poeciliid anatomy and for comparative data.

The work reported here is part of a larger survey of the fish fauna of Guatemala that has been carried on since 1963 with the generous support of Mr. James C. Greenway, Jr., who has provided a field vehicle for our

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use, made many necessary local arrangements for us in Guatemala, supplied funds for travel, equipment, and assistants, and who has given us much personal encouragement in our pursuit of the study. Dr. Reeve M. Bailey kindly read and criticized the manuscript of this paper.

SCOLICHTHYINI, NEW TRIBE

TYPE GENUS: *Scolichthys*, new genus.

DIAGNOSIS: This tribe is established to be equal in scope with the genus *Scolichthys* as diagnosed herein. The relationships and general attributes of the Scolichthyini are discussed below.

SCOLICHTHYS, NEW GENUS

TYPE SPECIES: *Scolichthys greenwayi*, new species.

DIAGNOSIS: In skull, parietals narrow, oval to subrectangular, not flaring posteriorly, extending along posterolateral margin of frontals; supraoccipital processes absent, or small when present; epiotic processes absent; posttemporal simple; marginal jaw teeth firmly attached to jaws, recurved, conical to somewhat flattened, and sharply or bluntly pointed; a narrow band of similar but smaller teeth behind marginal ones. Posterior pleural ribs in male bent sharply forward, their tips converging on but not in contact with pelvic girdle. Gonopodial suspensorium including three long, slender, rather straight gonapophyses, with prominent parapophyseal uncini arising from sharply antrorse proximal sections, anterior uncini small in all cases and posterior ones largest; ligastyle absent or occasionally represented by a minute ossicle, although suspensory ligament within which ligastyle forms in other poeciliids is quite long and well developed; primary gonactinostal complex with two deep notches dorsally, one between incorporated elements 2 and 3 and other between 3 and small superior lateral wings; inferior lateral wings only well developed, extending backward and outward away from midline. Gonopodium bilaterally symmetrical; segments of ray 3 not ankylosed and without spinous processes; ray 3 with a terminal pair of extremely long, slender, gently curved, and closely apposed antrorse segments which together form a style that projects well beyond gonopodial tip; stylar process and one or two preceding segments of ray 3 joined via an intervening wedge of nubbly calcified material with penultimate segments of ray 4a; ray 4a terminated by a claw-shaped median ossicle that invests a membranous, bluntly pointed terminal structure; ray 4a swollen subdistally into an elbow-like prominence that projects toward ray 3, with five to eight simple segments between "elbow" and terminal claw; tip of ray 4p in contact with

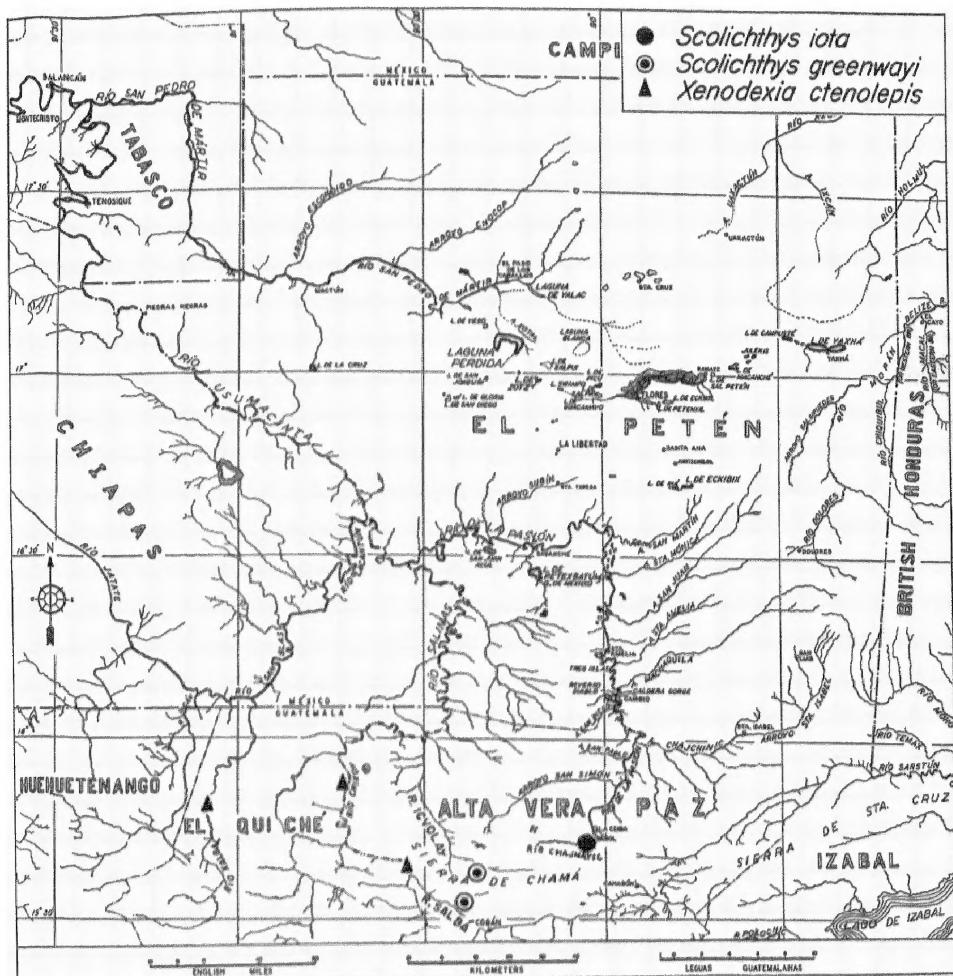


FIG. 1. El Petén, Guatemala, and adjacent regions, showing collecting localities in the upper parts of tributaries of the Río Usumacinta basin for *Scolichthys iota*, *S. greenwayi*, and *Xenodexia ctenolepis* Hubbs. The Río Xalbal record of *X. ctenolepis* is from a collection by K. D. Kallman and the writer in 1963, and the downstream record of *X. ctenolepis* in the Río Chixoy is from a collection by R. M. Bailey and the writer in 1966; the upstream Río Chixoy record is the type locality. The base map is modified from one compiled by Carl L. Hubbs and Henry van der Schalie in 1937.

claw of ray 4a with an elongate, very slender, and sinuous ultimate segment; ultimate segment of ray 4p preceded by eight to 12 retrorse serrae and five to seven simple subdistal segments which arch away from underlying ray 4a; tip of ray 5a touching penultimate segment of 4p; tip of ray 5p originating over fourth or fifth serra on ray 4p; rays 7 and 8 not in con-

tact at any point. Gonopodial length 37 to 43 per cent of standard length. Distance from dorsal fin origin to tip of snout 57 to 64 per cent of standard length.

COMPOSITION: The genus contains only the two species *greenwayi* and *iota*, described herein. The relationships of these species are discussed below.

ETYMOLOGY: The name *Scolichthys* is derived from the Greek *skolos* (masculine noun in the nominative singular) meaning "a thorn or prickle," and *ichthys*, in reference to the thornlike bony style at the tip of gonopodial ray 3 in the males of the two known species.

***Scolichthys greenwayi*, new species**

Figures 1-6

MATERIAL: The holotype (A.M.N.H. No. 22713) is an adult male,

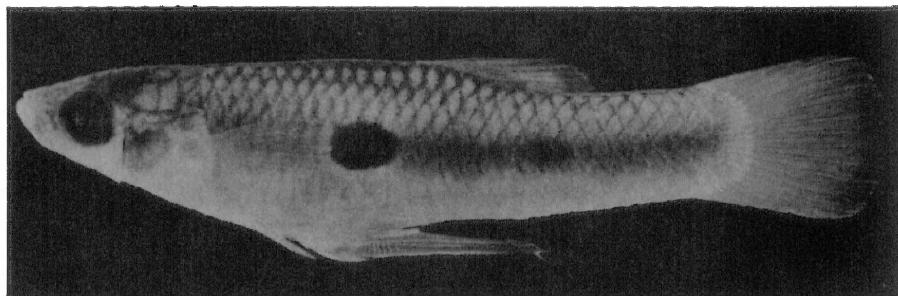


FIG. 2. Holotype of *Scolichthys greenwayi*, new species, A.M.N.H. No. 22713, an adult male 31.7 mm. in standard length.

31.7 mm. in standard length, obtained with rotenone in a clear, jungle, headwater stream of the Río Salbá, a tributary to the Río Chixoy-Río Salinas (Río Usumacinta basin), 20 kilometers northwest of Cobán and 6 to 8 kilometers north of Cancal, Alta Verapaz, Guatemala, on March 12, 1963, by Klaus D. Kallman and the writer. Taken with the holotype were 134 juveniles and adult males and females (A.M.N.H. No. 22714 + 22714WS). Additional specimens (55 juveniles and adult males and females, A.M.N.H. No. 22715) were obtained at Cubilguitz, Alta Verapaz, in a stream draining into the Río Dolores, tributary to the Río Icvolay which enters the Río Chixoy-Río Salinas about 100 kilometers downstream from the mouth of the Río Salbá, on April 2, 1963, by Kallman and the writer.

DIAGNOSIS: A species of *Scolichthys* of modest size (males ranging from about 16 to 30 mm. in standard length and females reaching nearly 50

mm.) with 12 pectoral rays and a striking color pattern (in preservative) of a dark blotch at midside overlying a diffuse, dusky, midlateral band. Life colors are described below. Gonopodium of male with bony style at tip of ray 3 longer than distance between "elbow" and "claw" on ray 4a; with about eight segments between "elbow" and "claw"; one or two definitive segments proximal to "elbow"; with a series of about eight terminal segments on ray 4p preceded by 10 to 12 retrorse serrae.

DESCRIPTION: Dorsal fin rays 9 (35); anal fin rays 10 (20); right pectoral rays 12 (35); scales in lateral series 29 (20), 30 (13), 31 (2). Measurements for males and females expressed as thousandths of the standard length; a range in values is followed by the arithmetic mean, in parentheses, for each of the two series collected, those from the Río Salbá (based on 10 males and 10 females) appearing first and the values for specimens from Cubilguitz (based on five males and 10 females) second.

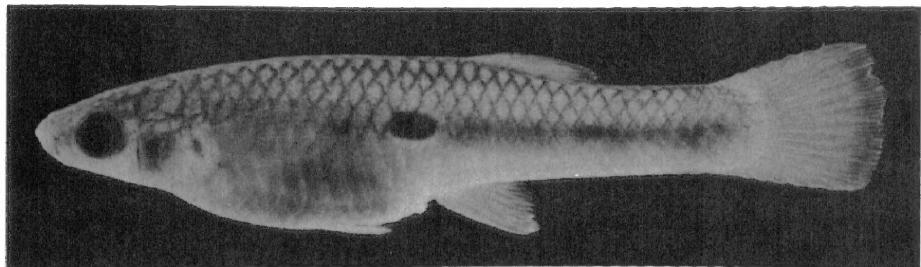


FIG. 3. Paratype of *Scolichthys greenwayi*, new species, A.M.N.H. No. 22714, an adult female 44.6 mm. in standard length.

Males (range of standard length in millimeters, Río Salbá: 20.5–31.4; Cubilguitz: 16.5–23.3): Greatest depth of body, 200–238 (213), 222–236 (230); least depth of caudal peduncle, 145–161 (152), 151–164 (154); dorsal fin origin to snout tip, 548–598 (573), 586–624 (602); anal fin origin to mandibular symphysis, 398–433 (422), 448–466 (454); head length, 239–274 (249), 266–279 (276); head width, 134–158 (143), 146–154 (151); snout length, 058–076 (069), 071–087 (077); orbit length, 069–088 (074), 086–097 (091); postorbital length of head, 095–122 (110), 107–115 (112); interorbital bony width, 083–093 (090), 099–107 (103); mouth, over-all width, 062–073 (068), 067–085 (076); gonopodial length, 348–381 (366), 387–405 (396); caudal fin length, 228–263 (246), 254–280 (265); pectoral fin length, 175–209 (189), 182–214 (192).

Females (range of standard length in millimeters, Río Salbá: 38.0–48.6; Cubilguitz: 26.9–42.5): Greatest depth of body, 192–221 (204), 194–218 (204); least depth of caudal peduncle, 115–139 (127), 123–141

(134); dorsal fin origin to snout tip, 601-618 (612), 609-653 (628); anal fin origin to mandibular symphysis, 557-592 (576), 574-612 (590); head length, 229-250 (238), 235-263 (256); head width, 144-160 (151), 151-163 (158); snout length, 066-085 (075), 061-072 (065); orbit length, 063-079 (068), 066-088 (077); postorbital length of head, 101-119 (108),

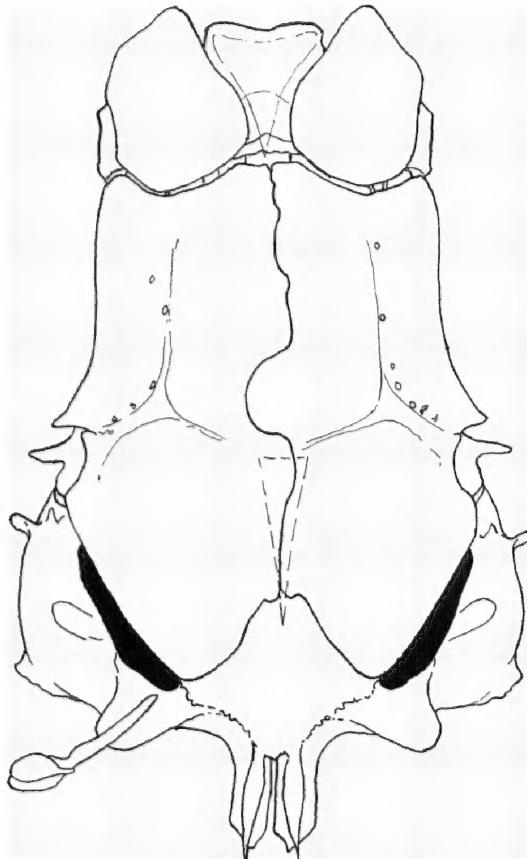


FIG. 4. Dorsocranum of adult male paratype of *Scolichthys greenwayi*, to show form of parietal bones (in black) and left posttemporal bone.

101-120 (112); interorbital bony width, 094-102 (100), 101-115 (109); mouth, over-all width, 061-072 (067), 072-086 (080); anal fin, depressed length, 175-195 (183), 191-205 (199); caudal fin length, 203-247 (224), 216-247 (235); pectoral fin length, 154-173 (163), 157-187 (174).

Scolichthys greenwayi is one of the most handsomely colored of all poeciliid species (fig. 2). The basic melanophore patterns on the body consist of (1) a heavy reticular network more or less restricted to the region above the midlateral scale row and extending from eye to caudal base, (2) a diffuse, dusky, midlateral stripe strongest on the caudal peduncle, (3) a large and elongate, somewhat ocellated, dark blotch on

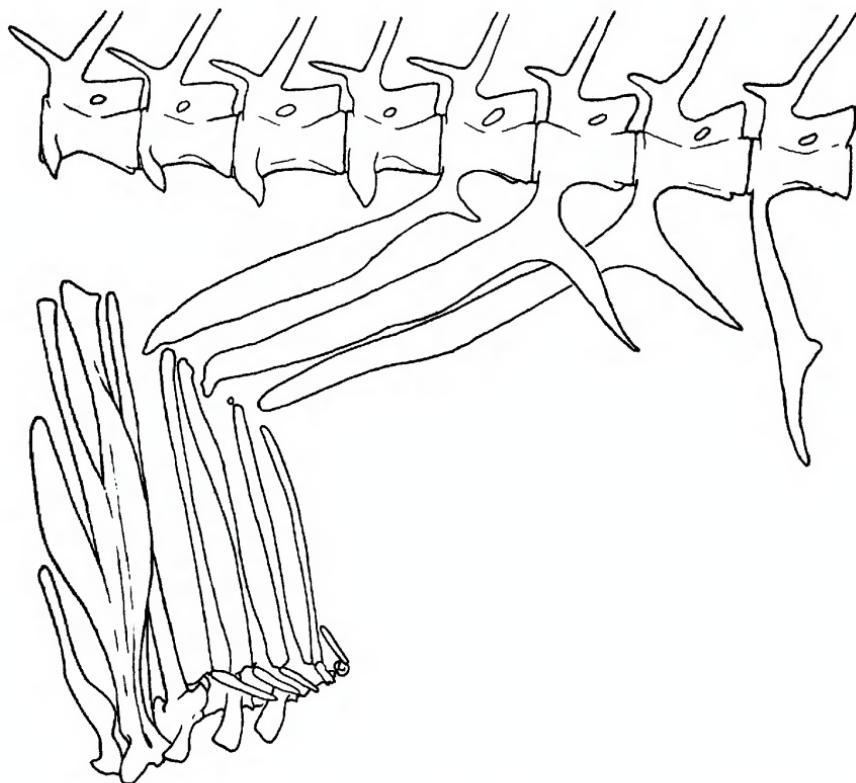


FIG. 5. Gonopodial suspensorium of adult male paratype of *Scolichthys greenwayi*.

the midlateral stripe just in front of a vertical from the dorsal fin origin, in many cases followed by one or more smaller and fainter blotches on the caudal peduncle, and (4) a dusky blotch of variable size, shape, and intensity on the pectoral fin base. Melanophore patterns on the fins consist mainly of a rather broad and diffuse distal or subdistal bar of dusky pigment along the posterior edge of the caudal fin, and a similar bar across the top of the dorsal fin below which, near the fin base, is a narrow, often darker, bar composed of discrete small blotches on the interradial membrane. Females usually have one or more small dark specks identifying the periproct and the base of the large genital papilla, and in both sexes there may be a light to moderate speckling of melanophores across the chin, snout, and cheeks, along the midventral line on the caudal peduncle, and along the fin rays of all fins. In both sexes the side below the midlateral dusky stripe is brilliant blue, the lower surface of the belly is lead white, the region around the periproct of the female and gonopodial base of the male is bright yellow, the anal fin (gono-

podium in male) has a light yellow wash, and the dorsal and caudal fins are bright orange-yellow.

Melanophore patterns in small young are distinctive, consisting, on the body, of three bars, the first, under the tip of the pectoral fin, being short and faint, the second in advance of the dorsal fin origin being broad, dark, bordered by light areas, and extending from midventral to middorsal line, and the third somewhat behind the dorsal fin, being as long as the second but narrow, not so dark, and not bordered by light areas. As the fish increase in size, the first bar gradually disappears, the second becomes shorter and broader, and the third becomes shorter. Males that differ-

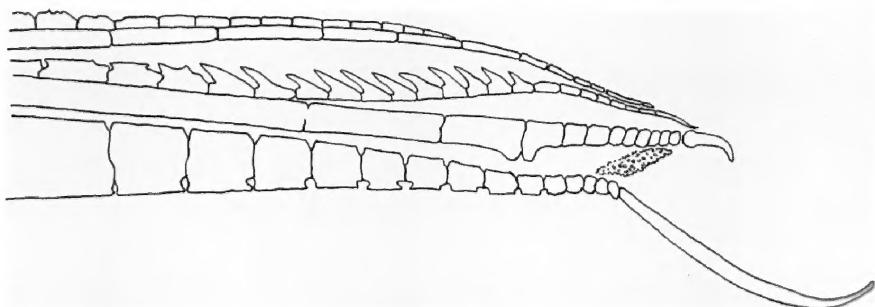


FIG. 6. Distal tip of gonopodium of adult male paratype of *Scolichthys greenwayi*.

tiate at a small size (up to 20 mm.) retain a more or less juvenile pattern of bars on the side, do not exhibit a midlateral dusky stripe, and have the dorsal and caudal fin bars only faintly developed.

It is noteworthy that in morphometry the Río Salbá and Cubilguitz populations differ in all but two characters, namely, in least depth of caudal peduncle and postorbital length of head. In addition, males of *S. greenwayi* from the two regions are not distinguishable in pectoral fin length, and females from these populations are identical in average greatest depth of body. All other morphometric traits of males and females of *S. greenwayi* from Cubilguitz exhibit a consistently higher average percentage of standard length than do those from the Río Salbá. There are at least three explanations for the differences. 1. The largest and mean sizes for each sex at Cubilguitz are noticeably less than those at Río Salbá, and the differences in body indices may reflect allometric growth patterns. 2. The specimens of *S. greenwayi* taken in Cubilguitz may have been ecophenotypes developing in a somewhat marginal habitat. Such a possibility is suggested by the fact that the Cubilguitz site is a surface stream of only a few hundred yards in extent, which originates in a large spring hole and meanders in shallow channels with a layer,

2 or 3 feet in depth, of flocculent, gray anaerobic mud bottom, to disappear again into the ground before joining the Río Dolores. The fish, when collected, appeared hollow-bellied, as did also some of the associated fish species which included the poeciliid *Xiphophorus helleri* and the cichlid *Cichlasoma intermediate*. If representatives of *S. greenwayi* exist in the Río Dolores proper, then it is possible that such individuals are as large and as robust as those in the Río Salbá. Finally, the different phenotypes of the two populations of *S. greenwayi* may reflect distinctively different genotypes, and, if this final possibility is demonstrated by laboratory or other study, the populations could readily be recognized as distinct subspecies. For the present, no considered explanation for the differences between the Cubilguitz and Río Salbá populations can be given.

ETYMOLOGY: The specific name *greenwayi* has been selected as an expression of gratitude to Mr. James C. Greenway, Jr., who has given to this work assistance and encouragement of every sort.

RANGE: Tributaries to the Río Chixoy (= Río Negro), Río Salinas system, Alta Verapaz, Guatemala (fig. 1).

Scolichthys iota, new species

Figures 1, 7-11

MATERIAL: The holotype (A.M.N.H. No. 22716) is an adult male, 16.3 mm. in standard length, obtained with rotenone in a tiny, clear creek emptying into the Río Chajmayic, the true headwater source of the Río de la Pasión (Río Usumacinta basin) 15 kilometers by road south of Sebol, Alta Verapaz, Guatemala, on March 14, 1963, by Klaus D. Kallman and the writer. Taken with the holotype were 142 juveniles and adult males and females (A.M.N.H. No. 22717+22717WS).

DIAGNOSIS: A diminutive species of *Scolichthys* (males of about 14 to 17 mm. in standard length and females reaching nearly 22 mm.) with 11 pectoral rays and a plain color pattern (in preservative and in life) of a reticular network overlying six to eight, short and faint dusky bars at midside anteriorly. Gonopodium of male with bony style at tip of ray 3 equal to or less than distance between "elbow" and "claw" on ray 4a; with about five segments between "elbow" and "claw"; "elbow" on a single, very long, unsegmented element; with a series of about six terminal segments on ray 4p preceded by eight or nine retrorse serrae.

DESCRIPTION: Dorsal fin rays 8 (1), 9 (17), 10 (1); anal fin rays 10 (10); right pectoral rays 11 (20); scales in lateral series 28 (1), 29 (17), 30 (1). Measurements for males and females expressed as thousandths of standard length; a range in values is followed by the arithmetic mean, in parentheses, for 10 males and 10 females.

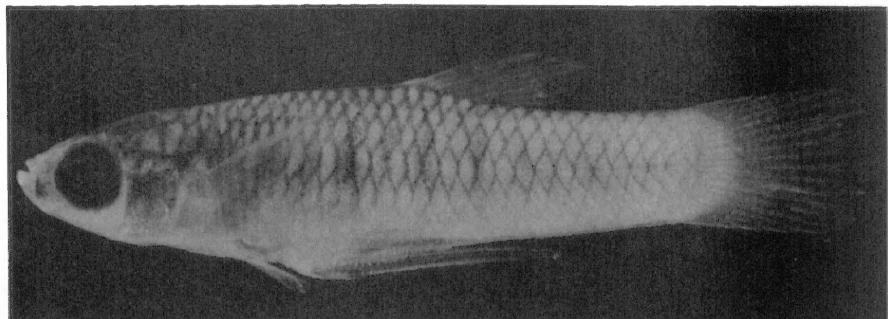


FIG. 7. Holotype of *Scolichthys iota*, new species, A.M.N.H. No. 22716, an adult male 16.3 mm. in standard length.

Males (range of standard length in millimeters: 14.4–15.1): Greatest depth of body, 221–248 (234); least depth of caudal peduncle, 159–168 (164); dorsal fin origin to snout tip, 576–600 (588); anal fin origin to mandibular symphysis, 430–462 (449); head length, 268–290 (277); head width, 160–173 (166); snout length, 066–073 (069); orbit length, 100–107 (104); postorbital length of head, 107–131 (120); interorbital bony width, 101–114 (109); mouth, over-all width, 067–087 (080); gonopodial length, 424–442 (432); caudal fin length, 298–317 (306); pectoral fin length, 187–220 (203).

Females (range of standard length in millimeters: 15.6–21.8): Greatest depth of body, 227–250 (236); least depth of caudal peduncle, 146–156 (151); dorsal fin origin to snout tip, 621–670 (638); anal fin origin to mandibular symphysis, 577–628 (601); head length, 270–317 (286); head width, 160–192 (178); snout length, 062–084 (075); orbit length, 089–108 (101); postorbital length of head, 108–122 (114); interorbital bony width, 110–128 (120); mouth, over-all width, 069–093 (083); anal fin, depressed

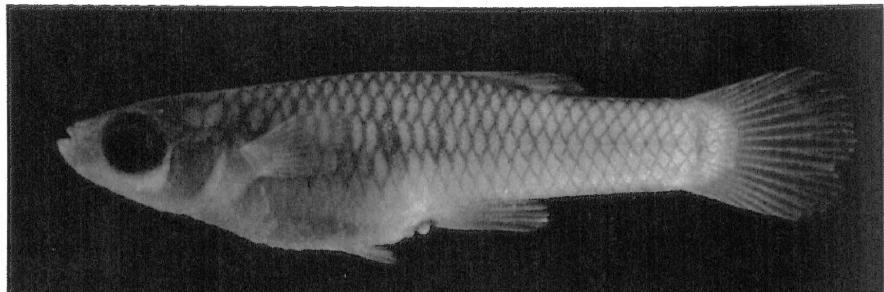


FIG. 8. Paratype of *Scolichthys iota*, new species, A.M.N.H. No. 22717, an adult female 21.8 mm. in standard length.

length, 189–214 (204); caudal fin length, 270–298 (288); pectoral fin length, 184–211 (195).

The obvious pigment patterns of *Scolichthys iota* are composed entirely of melanophores. On the body, they consist of (1) a reticular network covering all parts of the body except the lower surface of the belly and areas below and in front of the eye, (2) a series of four to 11, most often

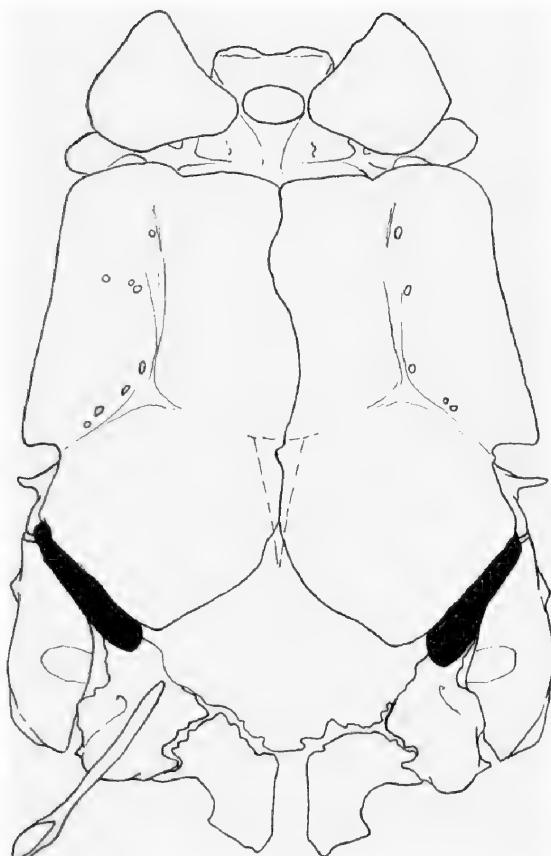


FIG. 9. Dorsocranum of adult male paratype of *Scolichthys iota*, to show form of parietal bones (in black) and left posttemporal bone.

eight, short, dusky bars at midside from opercular margin to caudal base, and (3), in the female, a very noticeable dark, elongate, periproctal spot. Most adult individuals have a blotch, as in *greenwayi*, on the pectoral fin base, but it is invariably very diffuse and usually faint when present. There is only slight indication of a dusky bar distally on the caudal and dorsal fins and of a narrow bar near the base of the dorsal, and these fin patterns are best appreciated when the fins are constricted or depressed. A dark line is present along the midventral edge of the caudal peduncle in both sexes.

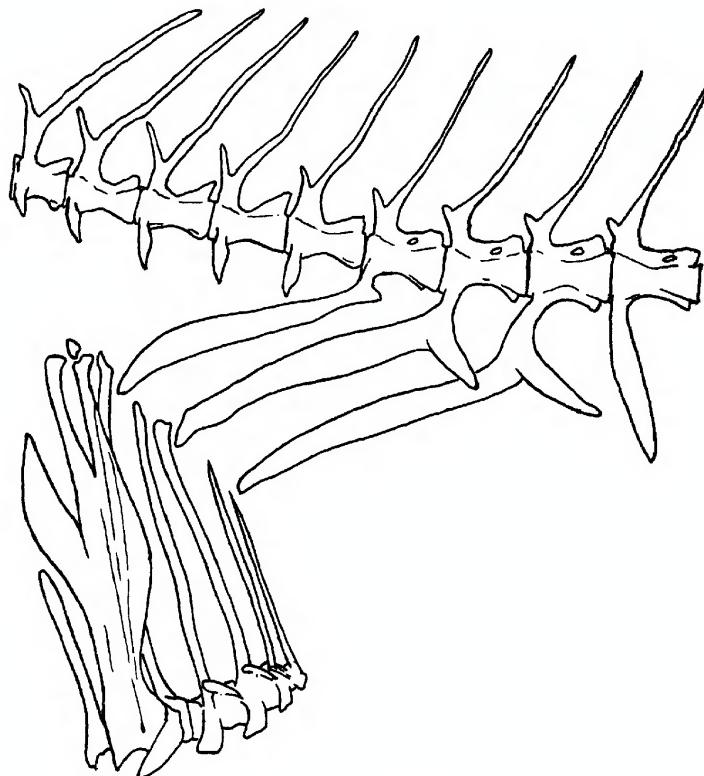


FIG. 10. Gonopodial suspensorium of adult male paratype of *Scolichthys iota*.

Half-grown individuals are marked only with a light reticulum and with five to eight evenly spaced, narrow, dusky bars across the side. Unfortunately, no really small juveniles were taken for comparison with the adults or with the juveniles of *greenwayi*.

ETYMOLOGY: The substantive *iota* (Greek, *ἰῶτα*, the smallest letter in the Greek alphabet) is employed in its figurative meaning (the least, or a very small, particle or quantity) in reference to the small size of this species.

RANGE: Río Chajmayic, the headwater source of the Río de la Pasión, Alta Verapaz, Guatemala (fig. 1).

RELATIONSHIPS OF SPECIES OF *SCOLICHTHYS* AND TAXONOMIC POSITION OF THE GENUS

Superficially the species of *Scolichthys*, especially *S. greenwayi*, most resemble the representatives of the cnesteroodontins of South America: *Cnesterodon*, *Phalloceros*, and *Phallotorynus*. The most noteworthy of these

similarities are in pigmentation (the black or blue-black spot on the trunk), in body and fin proportions (slender body, long caudal peduncle, dorsal fin origin only slightly nearer caudal base than snout tip, and long gonopodium), and in the presence on the tip of gonopodial ray 3 of a long antorse bony style and a clawlike element at the tip of ray 4a. Internally, the gonopodial suspensorium in *Scolichthys* is like that in *Phalloceros* or *Phallotorynus*, and in the new genus, in common with all cnesterodontins, *Phalloceros*, *Phallotorynus*, *Cnesterodon*, and *Phalloptychus*, the posttemporal is simple, without trace of a lower limb. The resemblances in suspensorial characters between the species of *Scolichthys* and those of

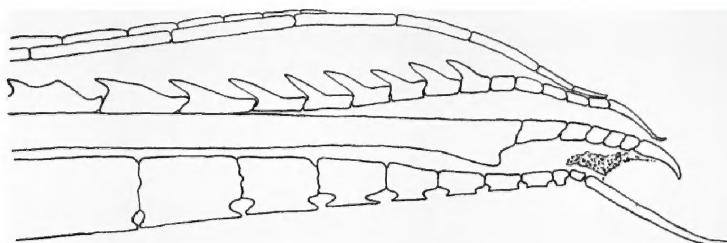


FIG. 11. Distal tip of gonopodium of adult male paratype of *Scolichthys iota*.

some of the Cnesterodontini reside chiefly in the dorsally excavated gonactinostal complex (certainly not a very trenchant feature), in the three elongate and rather straight, sharply inclined gonapophyses that bear parapophyseal uncini near their bent proximal portions, and in the elongate and sharply bent posterior pleural ribs that converge on (but do not touch) the pelvic girdle. The Central American heterandriins of the genus *Neoheterandria* have ribs modified in a similar way (although the ribs are greatly expanded anteroposteriorly in *Neoheterandria*), but, in each heterandriin genus, some or all species have diagnostic paired expansions on the shafts of the secondary gonactinosts, and such gonactinostal modifications are absent from *Scolichthys*. Moreover, the gonapophyses in the gonopodial suspensorium of heterandriins are usually sinuous and characteristically have large normal uncini (instead of the parapophyseal type as seen in cnesterodontins and the species of *Scolichthys*).

There are, however, important resemblances between the heterandriins and *Scolichthys* in some cranial and gonopodial characters. In both groups the premaxillae are robust bones, and the teeth are firmly rooted (in contrast to the smaller premaxillae and delicate movable teeth in cnesterodontins). The species of *Scolichthys* and most heterandriins have well-developed parietal bones (in cnesterodontins, these bones either are

wanting or they develop a peculiar sutured contact with the frontals). In having an antrorse bony style at the tip of gonopodial ray 3, the forms of *Scolichthys* resemble the heterandriin species *Priapichthys darienensis* and *P. choocoensis* from Panama and Colombia, respectively, and in the development of an "elbow" on ray 4a the forms of *Scolichthys* resemble those of *Neoheterandria*.

Hence, there appear to be a number of features in which the species of *Scolichthys* closely resemble both cnesteroodontins and members of the heterandriin genera *Neoheterandria* and *Priapichthys*. Because of these shared similarities and also because of certain entirely distinctive features (the absence of a ligastyle and the diagnostic combination of gonopodial characters), the species of *Scolichthys* appear, on the one hand, to tie together the Cnesteroodontini and Heterandriini and, on the other, to create a special problem in the taxonomic allocation of the new genus.

In addition to their anomalous morphological position in the family, the species of *Scolichthys* have certain zoogeographic peculiarities. *Scolichthys greenwayi*, for example, apparently is confined to headwater tributaries to the upper Río Chixoy (Río Salinas system) where it occurs together (although not sympatrically) with one of the two most distinctive and phylogenetically isolated members of the family, *Xenodexia ctenolepis* (the other being *Tomeurus gracilis* of northeastern South America). *Xenodexia*, but not *Scolichthys*, was also taken, in 1963, in the upper part of the Río Lacantún system in Guatemala (fig. 1). *Scolichthys iota* is at present known only from the Río Chajmayic, which is the headwater source of the Río de la Pasión. The Río Chajmayic passes under a mountain ridge before joining the Pasión, hence is isolated topographically from the main river. Other fish species besides *S. iota* appear to be endemic in the Río Chajmayic; among them (to be described in a forthcoming paper) are a new form of the poeciliid genus *Xiphophorus* and a form of the characin genus *Bramocharax* that has hitherto been reported only from the great lakes of Nicaragua. The apparent confinement of the species of *Scolichthys* to headland waters, their occurrence together with other extremely well-differentiated and similarly confined species, and the representation in an at least partly endemic fauna, all suggest that the genus is itself a relict of an old invasion of the Río Usumacinta basin that has been largely superseded except in the upper reaches of the three principal branch rivers—Río de la Pasión, Río Salinas, and Río Lacantún. The apparent relationships of *Scolichthys* to Central and South American poeciliids and the sympatry of one, *S. iota*, with the otherwise solely Nicaraguan *Bramocharax* seem to indicate that that invasion came from the south. This presumption, if valid, may mean that an ancient poeciliid radiation in

Central and northern South America, perhaps at a time when the Panamanian isthmus and neighboring regions formed an island archipelago, gave rise to two very distinctive lines, the eastern South American Cnesterodontini and the Central American and western South American representatives of the Heterandriini, and a third group that moved north on the Atlantic side to become, in the Río Usumacinta basin, the present-day *Scolichthys*. *Scolichthys* may have been eliminated subsequently in all but some isolated upland regions; the heterandriins may have undergone further diversification before spreading northward along both coasts of Middle America; and the connections across northern South America of the Cnesterodontini with their hypothetical lower Central American ancestors may have been severed by subsequent invasions of competing similar forms such as poeciliids of the tribe Poeciliini. That lower Central America and northern South America may have been near one of the ancient, principal poeciliid radiations is certainly suggested by the occurrence in eastern Venezuela, Guyana (formerly British Guiana), and Surinam to Para, Brazil, of the phyletically isolated and reproductively primitive poeciliid *Tomeurus gracilis*.

All the above conclusions and speculations on the relationships and origins of the species of *Scolichthys* seem to call for a revised tribal structure in the family, either in the union of the Cnesterodontini with the Heterandriini or the creation of a separate tribe to contain *Scolichthys*. Either course of action seems preferable to the arbitrary inclusion of *Scolichthys* in the Heterandriini on the basis of geographic proximity or in the Cnesterodontini because of a not impressively larger number of morphological resemblances. Moreover, including *Scolichthys* in the Cnesterodontini would be in conflict with some diagnostic cranial and gonopodial characters of that tribe, and its inclusion in the Heterandriini would be in conflict with the diagnostic suspensorial features of this tribe. If the two tribes are combined, the resulting larger category would be amorphous, and we are therefore left with the remaining alternative, adopted here, of erecting a new tribe, the Scolichthyini, which is co-extensive with the genus *Scolichthys*.

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